Short-term High Temperature Effects on Stomatal Behaviors of Rice Plants. I. Occurring at the Vegetative Stage[1]

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Abstract : In this study, the effects of a short period of high temperature (35 C, 8 days), relative to 25 C, occurring at the vegetative stage (Leaf 7 stage) on the seasonal changes of stomatal movements of rice plants (*Oryza sativa* L.) were investigated under controlled environment. The diurnal variations of stomatal pattern during the course of temperature changes were also monitored. The physiological importance of such effect was evaluated and discussed. Stomatal diffusive conductances of 35 C-treated plants were significantly higher than 25 C during the course of treatment, though the diurnal pattern of stomatal variations of both treatmints was observed. Instead of the phenomenon known as midday partial stomatal closure, the maximum conductance occurred at about noon (1400 h). Effect of temperature treatments may prolong up to Leaf 13 stage, which can be clearly discerned by plotting the data at 0800, 1400 and 2000 h. Stomatal conductance declined after heading as plants aged.

Key words : high temperature effects, stomatal behavior, rice, *Oryza sativa* L. vegetative stage, controlled environment.

Introduction

Stomatal movements are directly affected by temperature, an enverinmental variable that greatly comtributes to the growth, development and yield of plants. Changes of temperature may influence water relations of guard cells, which along with solute exchanges and mechanical interaction between guard cells and neighboring cells govern the opening and closing of stomata (Willmer, 1983). Indirectly, increase of temperature may affect internal crabon dioxide concentrations, caused by the outpace of respiration over photosynthesis, and the leaf-air vapor pressure deficit, resulting in plant water stress, that in turn affect stomatal movements.

Since the major role of stomata is to control entry of carbon dioxide for photosynthesis and to allow exit of water vapor in the process of transpiration, it is expected that the

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behavior of stomata in a leaf can affect the photosynthetic rate if water is not limited. Although Cowan and Farquhar (1977) have suggested that stomata may optimize gas exchange by maintaining a constant ratio of water loss against carbon assimilation, this balance may be jeopardized by an impact of high temperature. As temperature be raised, stomatal aperture will be stimulated due to the increase of the metabolic activity within the guard cells and the leaf as a whole. Beyond the range of optimal temperature stomata opening reduced as cell damage occurs.

Taniyama *et al.* (1987) reported that stomatal aperture of all cultivars of the tested rice plants reached a maximum at about midday both at active tillering stage and panicle initiation stage. Whereas, Ishihara and Saitoh (1987) and others (Tenhunen *et al.*, 1987; Turner *et al.*, 1978) have identified a midday depression of leaf gas exchange, especially in a hot, dry fine day and to those plants that are regularly subjected to drought. Yang and Heilman (1990b) observed a diurnal change of stomatal movements in the leaves of rice plants grown under controlled environment. Few researches have yet monitored the diurnal variations of stomatal movements of rice plants during the course of heat stress. Also, there is little information on the effect of a short-term high temperature, occurring at either vegetative or reproduvtive phase, upon the seasonal changes of stomatal behaviors in rice plants.

A serise of experiments were conducted in this study to examine the correlations between high temperature and stomatal movements in well-watered rice plants. The impact of a short period of heat stress to the long term stomatal behaviors was also investigated. This paper is emphasized on such effects imposing at the vegetative stage.

Materials and Methods

Plants of rice variety Lemont (Bollich *et al.*, 1984, 1985) were grown in opaque plastic containers (.25m diameter,. 20 m height, 0.049 m^2 surface area), filled with fritted clay. Three plants were grown per pot, with even space, and irrigated with nutrient solutions (see Yang and Heilman, 1990a). The plants were irrigated in excess twice a day, early morning and late afternoon, to keep the soil saturated. They were flushed with distilled water, every 7 days during the vegetative growth phase and every 3 days during the reproductive growth phase, to avoid salt accumulation. The pots were plugged in the center so that extra water was drained from the soil after irrigation.

The rice plants were grown as groups in a controlled-environment growth chamber with circulated ambient air (day/night temperatures 30 C/20 C ; relative humidity 55—70%/95—100%; CO_2 concentration 330—430 ppm).The daylength was 12 hours (0800—2000 h) with a PPFD (photosynthetic phonton flux density) of about 680 μmole m^{-2} s^{-1}. Wind speed was about 0.8 m s^{-1}. They were rotated periodically to ensure uniformity within the chamber.

When reaching the leaf 7 (L7) stage, plants were moved to an assimilation cabinet for 8-day temperature treatments (25C and 35 C),and then returned back to the growth chamber and grown to maturity. The assimilation cabinet was set for a photoperiod of 12

hours (0800—2000 h) and constant day/night temperatures (25C/25C or 35C/35C) and absolute humidity. Average wind speed was about 1 m s^{-1}. The average value of PPFD at the top of the cabinet, about 1 300 μmole m^{-2} s^{-1}, was provided by 'Ceramalux' lamps (Philips Corp., NJ; 400 W). Air timperature was measured by a dry- and wet-bulb psychrometer, which was placed adjacent to plant canopy and was controlled within ± 0.5 C.

The leaf stage (plant age) was assessed by the emergence of the primary leaf on the main culm (Yoshida, 1981). For example, when the 8th primary leaf emerges from the main culm, the plant is said to be at leaf 7 (L7) stage. Heading stage is the time period from the first day to the seventh day from heading; the R-1 (R1) stage is the time period from the 8th to the 14th day from heading, and so on. Stomatal (leaf) diffusive resistance was measured in the middle portion of the youngest fully expanded primary leaves by a porometer (MK3, Delta-T Devices, England). For diurnal data, the first measurement was taken at 0800 h, the onset of photoperiod, and the measurements were continued every two hours until 2000 h, the end of daytime hours. Stomatal conductance, the inverse of stomatal resistance, was used for analysis throughout this study. The mean values and standard deviations were taken from the averages of each group;at least four groups for each mean value.

Results

When plants were transferred from the growth chamber (day/night temperatures 30 C /20 C) to the assimilation cabinet (25 C/25 C), stomatal conductances declined until the fifth day of treatment (Figs. 1 and 2) as a result of changing growth. However, a reversed result was shown until the fifth day when plants were transferred to high temperature (35 C/35 C) cabinet (Fig. 2). There were considerable differences of stomatal conductance between the two temperature levels. Nevertheless, diurnal variations of stomatal conductance were observed in both treatments though data from 25 C were less distinctive than 35 C. Conductance was greatest at about 1400 h, the middle of photoperiod, during the treatment periods.

Monitoring of the diurnal variations of stomatal conductance after the treatments, from Leaf 8 stage to R-4 stage (Figs. 3 and 4), showed that temperature effects between treatments may extend up to Leaf 13 stage. This result is more clearly discerned from the conductances measured at 0800, 1400 and 2000 h as a function of stage of development as shown in figs. 5, 6 and 7. It was also shown that stomatal diffusive conductances declined after heading as plants aged.

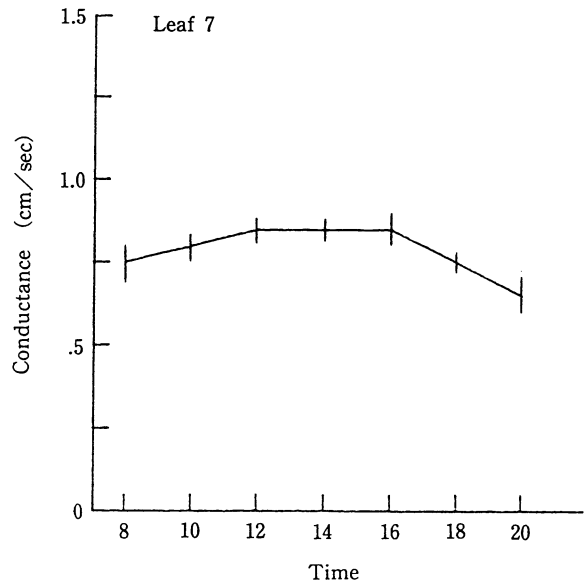

Fig 1. Stomatal conductances of Primary leaf 7 measured in the growth chamber (day/night temperatures 30 C/20 C) at the Leaf 7 stage. The measured primary leaf was the youngest fully expanded leaf. Standard deviation is included.

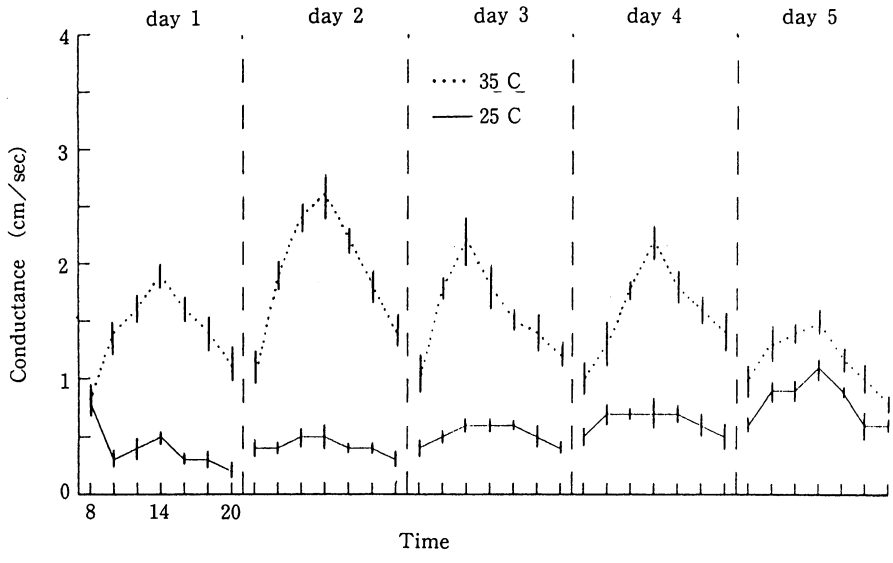

Fig 2. Effects of temperature treatments (35 C and 25 C) at the Leaf 7 stage on the diurnal changes of stomatal conductances of the 7th primary leaf. The measured primary leaf was the youngest fully expanded leaf. Standard deviation is included.

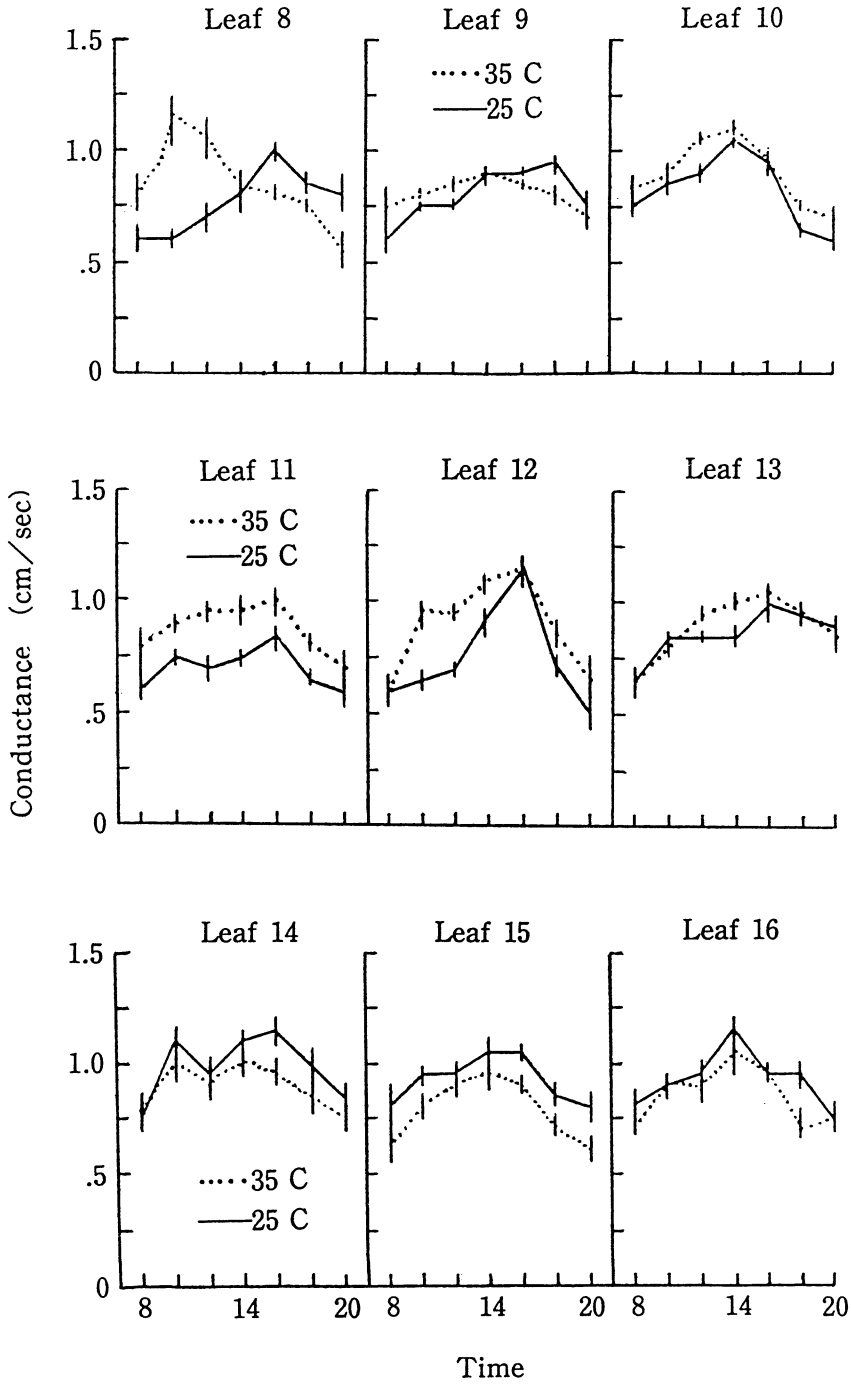

Fig 3. The diurnal changes of stomatal conductances of the primary leaves 8 to 16 as affected by 8-day temperature treatments imposed at the Leaf 7 stage. The measurements were taken at the corresponding stages. Standard deviation is included.

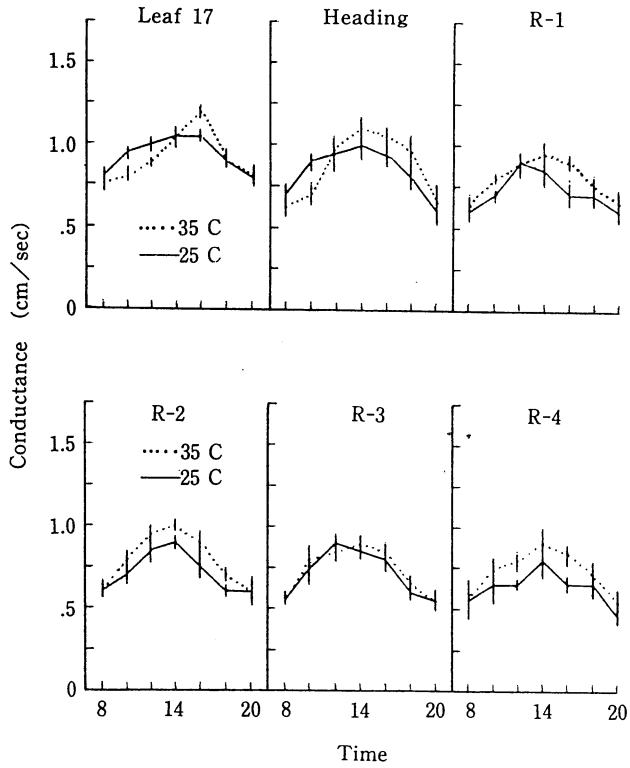

Fig 4. The diurnal changes of stomatal conductances of the 17th primary leaf at the leaf 17, heading,the R-1,the R-2, the R-3, and, the R-4 stages, as affected by 8-day temperature treatments imposed at the Leaf 7 stage. Standard deviation is included.

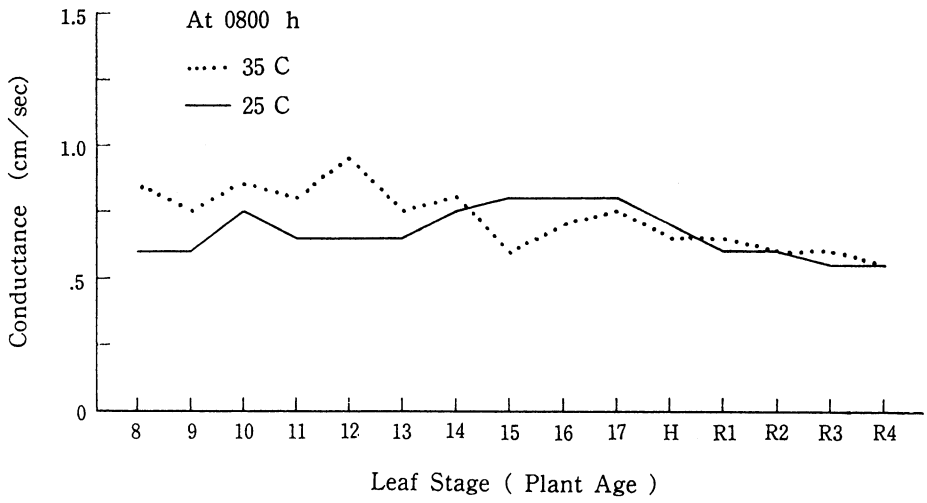

Fig 5. Stomatal conductances at 0800 h as functions of temperature and leaf stage (plant age).

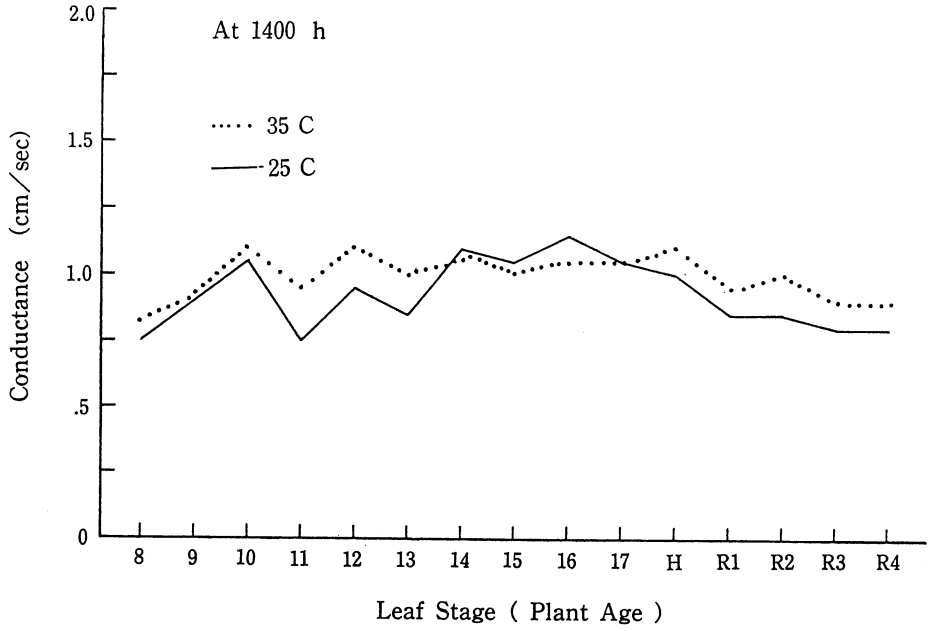

Fig 6. Stomatal conductances at 1400 h as functions of temperature and legf stage (plant age).

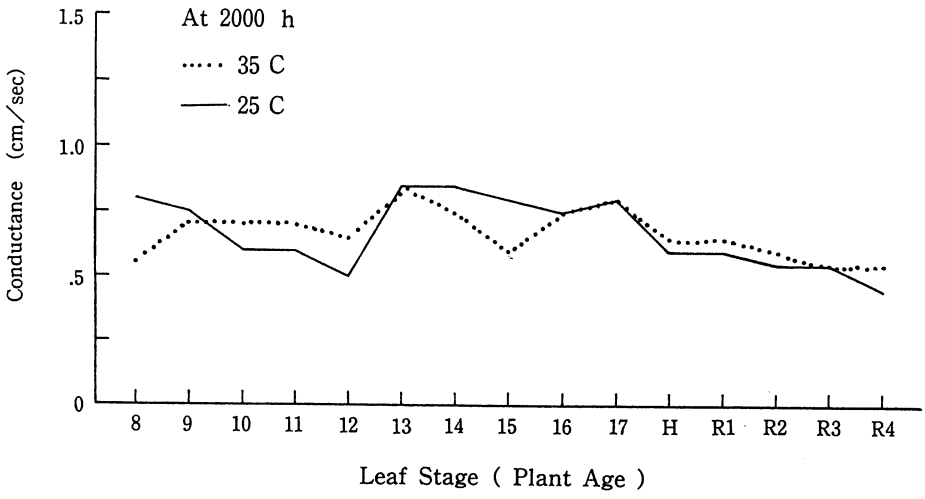

Fig 7. Stomatal conductances at 2000 h as functions of temperature and legf stage (plant age).

Discussion

Diurnal changes of stomatal movements were observed in rice plants under controlled environment. Whereas, stomatal opening was stimulated at 35 C though diurnal patterns were preserved. This behavior is similar to rice grown under natural conditions (Tenhunen *et al.*, 1987) and also for field-grown rice varieties (Kawamitsu and Agata, 1987; Ishihara and Saitoh, 1987). As Willmer (1983) pointed out, increased stomatal conductance due to high temperature may enhance gas exchanges in favor of photosynthesis and evaporative cooling of the leaf and improve the transpiration stream for ion uptaks and transport. However, the demand for metabolic activities, the loss of water in increasing transpiration rate, and the damage to cells and growing processes may offset the advantages and result in a detrimental effect, especially when such heat stress is prolonged.

The relationship between leaf conductance and net photosynthesis is closely correlated (Wong *et al.*, 1979; Korner *et al.*, 1979). From linear regression, a close correlation between stomatal conductance and photosynthetic rate was found in rice plants (Kawamitsu and Agata, 1987). The same conclusion was also made by others (Ishihara and Saitoh, 1987; Ishii *et al.*, 1977). More works, however, need to be done to elucidate increase of stomatal conductance in relation to the counterbalance of photosynthesis and respiration during treatment period.

The phenomenon known as midday stomatal closure was not observed in this case, which may be due to a well-watered plants and the control of absolute air humidity in the growth chamber. Taniyama *et al.* (1987) reported similar results in the tested rice cultivars, while Ishihara and Saitoh (1987) showed that leaf stomatal aperture of rice plant decreased in fine day with high evaporative demand under submerged condition in the field.

Effects of 8-day temperature treatments on stomatal behavior was found to extend up to leaf 13 stage. The result was more clearly discerned at 0800, 1400 and 2000 h. Whether such effects have a significant impact upon growth and development of rice plants needs to be further studied. The decrease of conductances after heading is no surprise since the senescence of the measured leaf as well as plant canopy was in progress.

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短期高溫處理對水稻氣孔表現之效應. I. 營養生長時期[1]

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摘 要

本文旨在控制環境下探討水稻（*Oryza sativa* L.）營養生長期間短期高溫處理（35°C，8天）後氣孔運動之季節性表現，並調查處理期間氣孔每日週期性變化，以瞭解和評估高溫對水稻氣孔行爲及生理上之影響。結果顯示，高溫雖然提高氣孔傳導度，但不影響其每日週期性變化。氣孔傳導度在中午達到最高點，因此所謂午間氣孔部份關閉現象並未發現。結果亦顯示，營養生長初期（第7葉齡期）短期（8天）溫度處理之效應可達至第13葉齡期。至幼穗形成期時，氣孔傳導度顯著升高，此一結果可能爲植株追求高光合成需要所產生之自身調節，且不受第七葉齡期短期高溫處理之影響。本試驗同時證明，水稻葉片在控制環境下具有氣孔運動。

關鍵詞：高溫處理，氣孔行爲，水稻，*Oryza sativa* L.，營養生長期間，控制環境。

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